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CLASSIFICATION AND ORDINATION OF
ALPINE PLANT COMMUNITIES, SHEEP MOUNTAIN,
LEMHI COUNTY, IDAHO

A Thesis

Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
in the
College of Graduate Studies
University of Idaho

by

Stephan M. Urbanczyk

April 1993

Major Professor: Douglass M. Henderson, Ph.D.

AUTHORIZATION TO SUBMIT
THESIS

This thesis of Stephan M. Urbanczyk, submitted for the degree of Master of Science with a major in Botany and titled "Classification and Ordination of Alpine Plant Communities, Sheep Mountain, Lemhi County, Idaho," has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

The alpine vegetation in the immediate vicinity of Sheep Mountain, Lemhi Range, Lemhi County, Idaho, was investigated using data from field observations analyzed by the programs TWINSpan and CANOCO (CCA). Percent cover of vegetation and environmental data were recorded for 77 plots. By computer analysis, eight communities were identified and then described with respect to apparent habitat preferences. The predominant communities are characterized by a) *Carex rupestris*, b) *Carex elynoides*, and c) *Calamagrostis purpurascens*-*Carex elynoides*. An exposure gradient showed the strongest correlation with the community distribution, but substrate, elevation, and slope were also found to be important. In general, the study area communities present a uniformly dry turf-like physiognomy, with some early snowbed and *Dryas* or *Salix* mat communities occasionally present.

ACKNOWLEDGEMENTS

I am grateful for the help and guidance provided by my Major Professor, Dr. Douglass M. Henderson. My work is a small addition to the impressive collection of information on the flora of east-central Idaho that he has personally gathered, or has inspired others to seek. He is a master of the art of teaching and should be justly proud of that talent.

I would also like to thank the members of my committee, Dr. Anne W. Sylvester and Dr. Donald C. Thill, for their many helpful suggestions and criticisms. This research was supported by a grant from the Stillinger Fund for Forestry and Botanical Research.

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INTRODUCTION

Alpine, for the purposes of this research, is defined as the vegetation above naturally occurring upper timberline. While there has been some disagreement in the literature over what to include in an alpine study, I have chosen to follow the alpine definition of Billings (1974) and the research examples of Del Moral (1979), Hrapko and La Roi (1978), and Komárková and Webber (1978) by not including krummholz in the present study. Krummholz is the area of sparse, dwarfed trees that mark the transition from subalpine forest to the treeless alpine vegetation. Some of the stands sampled were at lower or equal elevations as krummholz trees, but were displaced from the trees by at least 15 meters.

Alpine areas are characterized by environmental extremes, such as cold temperatures, high winds, persistent snow cover, and unstable soil. In combination with an abruptly changing topography, these factors create a highly variable and intricate vegetation pattern. Fortunately, the pattern can be readily observed due to the typically short stature of alpine plants (Bliss 1963). Most alpine species have a perennial, herbaceous habit, with a growth-form that varies from a cushion plant in the exposed locations to a graminoid appearance in the mesic sites, although dwarf shrubs are also common (Billings 1974). Annuals are rare in the alpine, none of which were found in my study area.

Idaho alpine studies have been few in number and have only recently been accomplished. Many alpine areas within the state remain to be investigated before a clear picture of Idaho alpine can be assembled. Based on previous brief field observations of Sheep Mountain by Dr. Henderson, University of Idaho Herbarium, and the variability in topography and substrate of the location, Sheep Mountain was predicted to have a variety of alpine communities, some possibly unique, and was expected to provide a substantial

amount of information on Idaho alpine for the field effort expended. To test this hypothesis, I have conducted research on Sheep Mountain with the following objectives:

1. Sample and record alpine plant composition and cover as well as observable environmental data;
2. Analyze the data using multivariate analysis to detect natural communities and environmental gradients;
3. Correlate the outcome of analysis with available literature with special emphasis on Idaho alpine studies; and
4. Document the study with voucher specimens deposited in the University of Idaho Herbarium.

The following section is a description of my research written in journal format. All literature references in that section are listed in the "Literature Cited" entry of the journal paper. Several appendices have been added to expand on selected areas of the journal paper and to provide additional collection and analysis information not necessarily appropriate for inclusion in a journal paper. All literature references in this introduction, as well as in the appendices, are listed in Appendix 1.

JOURNAL PAPER

CLASSIFICATION AND ORDINATION OF
ALPINE PLANT COMMUNITIES, SHEEP MOUNTAIN,
LEMHI COUNTY, IDAHO

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ABSTRACT

The alpine vegetation in the immediate vicinity of Sheep Mountain, Lemhi Range, Lemhi County, Idaho, was investigated using data from field observations analyzed by the programs TWINSpan and CANOCO (CCA). Percent cover of vegetation and environmental data were recorded for 77 plots. By computer analysis, eight communities were identified and then described with respect to apparent habitat preferences. The predominant communities are characterized by a) *Carex rupestris*, b) *Carex elynoides*, and c) *Calamagrostis purpurascens*-*Carex elynoides*. An exposure gradient showed the strongest correlation with the community distribution, but substrate, elevation, and slope were also found to be important. In general, the study area communities present a uniformly dry turf-like physiognomy, with some early snowbed and *Dryas* or *Salix* mat communities occasionally present.

In the last few decades, many alpine studies have been published, but of all the alpine areas in North America, Idaho alpine has received the least attention. Until

recently, it was not common knowledge that Idaho has well-developed alpine communities, but this and other studies document its existence. Our observations are supported by numerous collections and studies of several researchers dating back to the 1800's. Thomas Nuttall may have made alpine collections in Idaho as early as 1834 (Mckelvey 1955), followed by L. F. Henderson (1890's) and C. Leo Hitchcock and Clarence Muhlek (1940's and 50's) (Henderson, in press). The junior author and students associated with the University of Idaho Herbarium have been collecting in and studying the east-central Idaho alpine since 1973. Brunsfeld (1981) completed an alpine flora for part of east-central Idaho based on collections from the Lost River and southern Lemhi ranges, and the southern Beaverhead Mountains. Caicco (1983) and Moseley (1985) have each completed community studies for selected sites in east-central Idaho.

From these collections and studies, as well as from field observations of the junior author, Idaho alpine appears to be restricted to the mountains of central and east-central Idaho. The present research area, Sheep Mountain, is located in the southern Lemhi Range, about 32 km south of Leadore. The Sheep Mountain alpine is in excellent condition, and the site has been accepted as a candidate Research Natural Area by the Forest Service (Wellner, in prep.).

Other Idaho alpine studies (Caicco 1983, Moseley 1985) have documented all of the general categories of alpine communities typically seen in temperate alpine locations, e.g. fellfield, turf, meadow, and bog. Based on those studies, field observations by the junior author, and the topographic and substrate variety of Sheep Mountain, we predicted that Sheep Mountain would also have a wide variety of alpine communities, some possibly unique. To test this prediction, we sampled the Sheep Mountain alpine

vegetation with the goals of classifying the plant communities, describing their distribution with respect to measured environmental variables, and relating the results of the analysis to several regional studies.

STUDY AREA

The proposed Sheep Mountain Research Natural Area (RNA) (44°22'N, 113°16'W) (Fig. 1) is centered along the crest of the southeast trending Lemhi Range, and encompasses 3.2 km of ridgeline (Wellner, in prep.). Elevations of the RNA range from 3000 to 3312 m, includes approximately 220 ha, and, except for scattered individuals of *Pinus albicaulus* Engelm. in a few locations to 3025 m, the area is dominated by alpine vegetation. Sixty-six of the 77 plots sampled were located in the RNA; the other 11 were placed 0.8 km to the south on the north slope of Spring Mountain (Fig. 1). Timberline in both locations is composed of *Pinus albicaulis* and *Juniperis communis* L. associated with *Festuca ovina* var. *ingrata* Hackel ex Beal and *Artemisia tridentata* Nutt. Access is provided by primitive roads originating in Squaw Creek Canyon on the west side and Spring Mountain Canyon on the east.

Two parent rock materials are exposed in the area, dolomite and quartzite (Ruppel and Lopez 1981), with abrupt transitions between each. Most of the soil is derived from dolomite, except for a few isolated bands where the parent material is quartzite.

Climatic data were not directly measured, but were estimated from regional weather stations (Myron Molnau, Office of State Climatologist, pers. comm.). Temperature information originates from Leadore, Idaho, elevation 1829 m, 32 km north, and was corrected for elevation (0.64° C/100 m). The coldest month is January with an average temperature of -16° C, while the warmest month is July at 9° C. Precipitation for the study area is assumed to be similar to Meadow Lake, 6.4 km to the north; total precipitation for the year is 853 mm; a unimodal pattern is evident, with the majority of moisture falling during the winter months, 110 mm falling in January alone. The summer

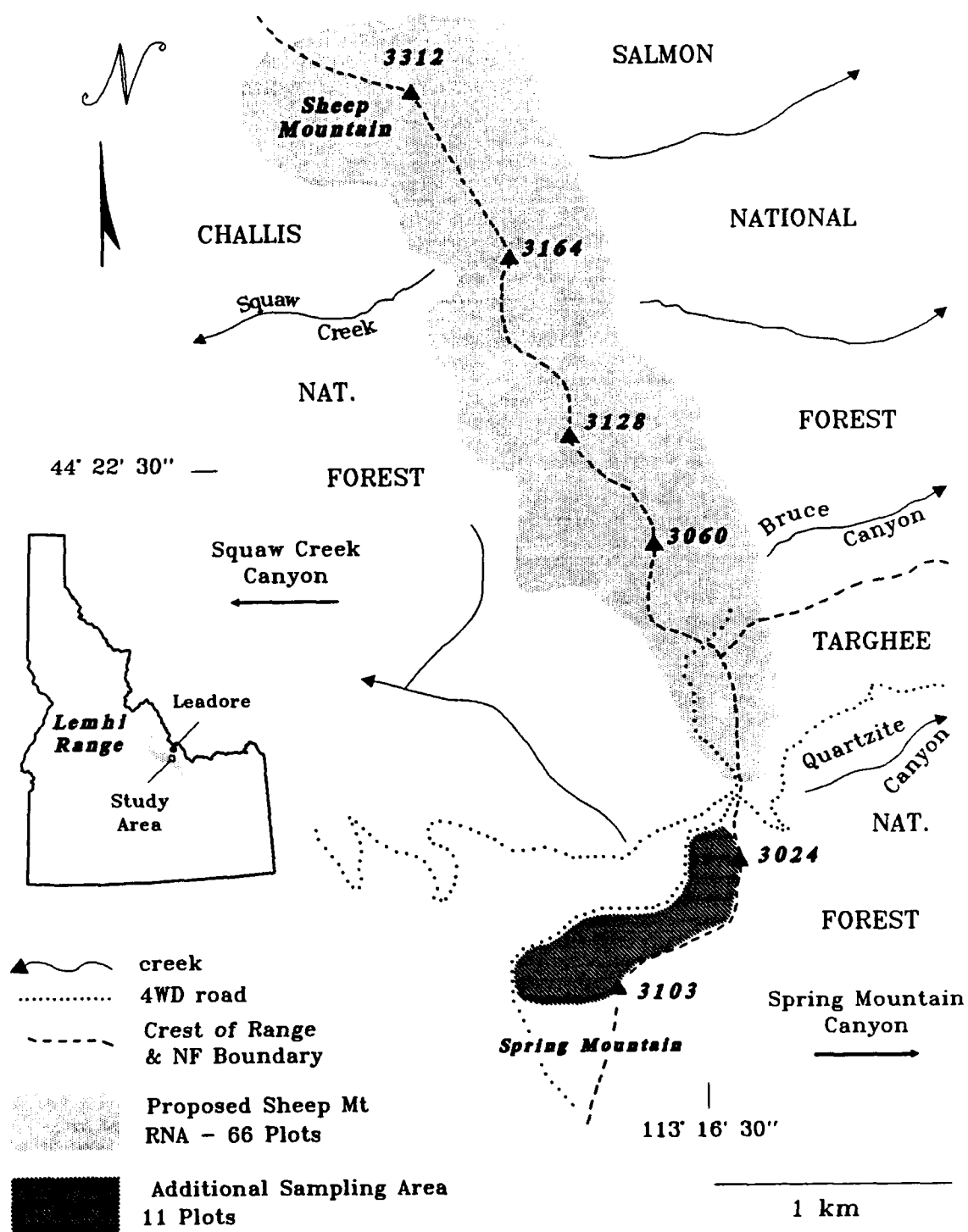


Fig. 1. Study area location. Altitudes are in meters.

months are generally dry, with only 27 mm falling in July as occasional rainshowers.

Overall, the area has a mountain climate with both coastal and continental influences and prevailing winds from the west (Ross and Savage 1967) resulting in cold, wet winters, and warm, dry summers. All vegetation sampled was clear of snow by 21 June 1992 when sampling began, although lingering snowbanks were present in places.

Land use history includes mostly mining exploration, with apparently little grazing (Wellner, in prep.). The remains of several small mines or pits are evident, but they only insignificantly scar the area. The absence of grazing dates back at least twenty years (Steve Spencer, Range Management, Lost River Range District, pers. comm.).

METHODS

Data collection (see Appendix 1 for additional discussion). Fieldwork was conducted from 21 June to 25 July 1992. Only vegetation above treeline and krummholz was examined. Seventy-seven plots were sampled using the methods of Bliss (1963) and Douglas and Bliss (1977). The process begins with the identification of a homogeneous stand of alpine plants no less than 60 m² in size. Within the stand a plot 4 by 8 m is measured and then further divided into eight rows, each 4 by 1 m. Replicate plots are sampled if permitted by the size of the stand. Four of the rows are randomly selected to be sampled by five quadrats, each 0.2 by 0.5 m and spaced at 0.5 m intervals. If an odd row is selected, the first quadrat is placed adjacent to the edge of the plot; whereas in an even row, the first quadrat is displaced 0.5 m. The end result is 20 quadrats with a combined area of 2 m².

For each of the quadrats, the percent cover for all of the species was estimated visually using the quadrat methods of Daubenmire (1959). The plot cover for a species was the average of the 20 quadrats. Environmental information was recorded for each plot and included location, elevation, slope, substrate, and exposure index. Elevation information was calculated from a United States Geological Survey 7.5' map of the Gilmore and Big Windy Peak Quadrangles. Plot substrate was identified by rock samples examined by Dr. William Rember (Department of Geology, University of Idaho). The exposure index consisted of a scale from 1 to 5, 1 being a low exposure, and reflected several environmental factors at once (Del Moral 1979). The factors considered were slope and aspect (measured by Brunton Pocket Transit), position on ridge, substrate, soil development, soil consistency, and snow/drainage patterns.

Specimens were collected, pressed, identified, and deposited in the University of Idaho Herbarium (ID). Nomenclature follows Hitchcock and Cronquist (1973) except for the Poaceae (Welsh et al. 1987), and *Cymopteris douglassii* R. L. Hartman et Constance (Hartman and Constance 1985).

Data analysis (see Appendix 1 for additional discussion). Only plants with greater than 2% cover in one or more plots were considered for analysis (Table 1); in all, 38 species were included. TWINSpan (Hill 1979), with default species cutlevels, was used to derive a classification, and canonical correspondence analysis (CCA), as implemented by the program CANOCO (Ter Braak 1987-1992) and with species data transformed to the Octave Scale (Gauch 1977), provided an ordination. Deletion of rare species, as suggested by Gauch (1982), was attempted, but was found to have no effect on the overall interpretation; the complete data set was retained.

TWINSpan is a hierarchical classification program that uses reciprocal averaging repeatedly to divide the data set into smaller and smaller groups (Hill 1979). Analysis was accomplished with default values in place. The resulting dendrogram was interpreted with respect to field observations and measured environmental variables, with described groups being derived from several levels in the hierarchy.

CCA uses reciprocal averaging constrained by environmental information (Ter Braak 1987). The axes are required to be linear combinations of the measured environmental factors. In short, reciprocal averaging is transformed from an indirect to a direct gradient analysis. An eigenvalue (λ) for each axis indicates the variation of the species data explained by that axis; the larger the eigenvalue, the larger the dispersion of species scores along the axis. When plotted, species scores are derived from the weighted

TABLE 1. LIST OF PLANTS USED IN TWINSPLAN AND CCA ANALYSIS AND ASSOCIATED ABBREVIATIONS DISPLAYED IN DENDROGRAM (FIG. 2) AND SPECIES ORDINATION DIAGRAM (FIG. 4). ALL SPECIES WERE PRESENT IN AT LEAST ONE PLOT AT GREATER THAN 2% COVER.

Species	Abbreviations
<i>Achillea millefolium</i> L. var. <i>alpicola</i> (Rydb.) Garrett	Ach mil
<i>Agoseris glauca</i> (Pursh) Raf. var. <i>dasycephala</i> (T. & G.) Jeps.	Ago gla
<i>Anemone multifida</i> Poir. var. <i>tetonensis</i> (Porter) Hitchc.	Ane mul
<i>Antennaria lanata</i> (Hook.) Greene	Ant lan
<i>Antennaria umbrinella</i> Rydb.	Ant umb
<i>Arenaria congesta</i> Nutt. var. <i>cephaloidea</i> (Rydb.) McGuire	Are con
<i>Arenaria obtusiloba</i> (Rydb.) Fern.	Are obt
<i>Astragalus kentrophyta</i> Gray var. <i>implexus</i> (Canby) Barneby	Ast ken
<i>Calamagrostis purpurascens</i> R. Br.	Cal pur
<i>Carex elynoides</i> Holm.	Car ely
<i>Carex rupestris</i> All.	Car rup
<i>Cymopterus douglassii</i> R.L. Hartman et Constance	Cym dou
<i>Cymopterus nivalis</i> Wats.	Cym niv
<i>Dryas octopetala</i> L. var. <i>hookeriana</i> (Juz.) Breit	Dry oct
<i>Elymus spicatus</i> (Pursh) Gould	Ely spi
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	Ely tra
<i>Erigeron compositus</i> Pursh var. <i>glabratus</i> Macoun	Eri com
<i>Eritrichium nanum</i> (Vill.) Schrad. var. <i>elongatum</i> (Rydb.) Cronq.	Eri nan
<i>Festuca ovina</i> L. var. <i>brevifolia</i> (R.Br.) Wats.	Fes ovi
<i>Frasera speciosa</i> Dougl.	Fra spe
<i>Haplopappus acaulis</i> (Nutt.) Gray	Hap aca
<i>Hymenoxys grandiflora</i> (T. & G.) Parker	Hym gra
<i>Leucopoa kingii</i> (S. Wats.) Weber	Leu kin
<i>Lloydia serotina</i> (L.) Sweet.	Llo ser
<i>Lupinus argenteus</i> Pursh var. <i>depressus</i> (Rydb.) Hitchc.	Lup arg
<i>Oxytropis besseyii</i> (Rydb.) Blank. var. <i>argophylla</i> (Rydb.) Barneby	Oxy bes
<i>Penstemon attenuatus</i> Dougl. var. <i>pseudoprocerus</i> (Rydb.) Cronq.	Pen att
<i>Phlox multiflora</i> A. Nels.	Phl mul
<i>Phlox pulvinata</i> (Wherry) Cronq.	Phl pul
<i>Potentilla diversifolia</i> Lehm.	Pot div
<i>Potentilla ovina</i> Macoun	Pot ovi
<i>Salix nivalis</i> Hook. var. <i>nivalis</i>	Sal niv
<i>Selaginella densa</i> Rydb.	Sel den
<i>Silene repens</i> Pers.	Sil rep
<i>Solidago multiradiata</i> Ait. var. <i>scopulorum</i> Gray	Sol mul
<i>Synthyris pinnatifida</i> Wats. var. <i>canescens</i> (Pennel) Cronq.	Syn pin
<i>Trifolium haydenii</i> Porter	Tri hay
<i>Zigadenus elegans</i> Pursh	Zig ele

averages of site scores. Arrows in the diagram represent the direction of variation of an environmental variable. Sites perpendicularly projected onto the arrows provide a rank ordering of the sites for that environmental variable. The same can be said of the species, except the rank ordering is of the weighted averages of site environmental values of sites containing that species. The mean of an environmental variable is represented by the origin, so that the arrowhead side has the interpretation of being above average and the opposite for the tail side of the arrow. The length of the arrow indicates how well the environmental variable is correlated with the pattern in the ordination diagram. Nominal variables or classes, in this analysis, substrate, are represented as points and are positioned so as to be the weighted average of the site scores of the sites belonging to that class. Each environmental variable also has a correlation coefficient (r) for each axis, which numerically indicates how well that environmental variable helps explain the observed variation on the axis. Overall variation explained by the illustrated ordination is determined by adding the eigenvalues for the axes and dividing by the total of the constrained eigenvalues.

RESULTS

TWINSPAN analysis (Fig. 2) of the data set suggests eight groupings: 1) *Salix nivalis*, 2) *Solidago multiradiata-Trifolium haydenii*, 3) *Carex elynoides-Trifolium haydenii*, 4) *Carex elynoides*, 5) *Calamagrostis purpurascens-Carex elynoides*, 6) *Carex rupestris*, 7) *Dryas octopetala*, and 8) *Leucopoa kingii*. The first division ($e = 0.492$) separates the *Leucopoa kingii* communities (Group 8) from the rest. The second division ($e = 0.471$) primarily distinguishes the more exposed, drier, or steeper sites (Groups 5, 6, and 7) from the more mesic, sheltered sites (Groups 1, 2, 3, and 4). Division 3 ($e = 0.527$) is again along an exposure gradient, with the *Carex elynoides* turf community (Group 4) being separated from the less exposed, winter snow-covered or early snowbed communities (Groups 1, 2, and 3). Additional divisions of the latter (Division 5, $e = 0.593$; Division 7, $e = 0.501$) appear to be associated with date of snowmelt, the *Carex elynoides-Trifolium haydenii* community (Group 3) being free of snow first, followed by the other two (Groups 1 and 2). The *Solidago multiradiata-Trifolium haydenii* community (Group 2) was in an obvious snow-collecting depression, but was free of snow by 21 June. The *Salix nivalis* community (Group 1) was also free of snow, but was fed by an adjacent snowbank.

The CCA ordinations for plots and species are depicted in Figs. 3 and 4. The first axis ($e = 0.45$) was primarily correlated with the exposure index ($r = -0.98$), but also partially with elevation ($r = -0.56$). The second axis ($e = 0.30$) was correlated with substrate (dolomite, $r = -0.87$; quartz, $r = 0.87$; mixed, $r = 0.09$) and elevation ($r = -0.58$). The third axis ($e = 0.22$) was correlated only with slope ($r = 0.92$) (see Appendix 4). Overall, the species and plot ordination diagrams, utilizing the first two

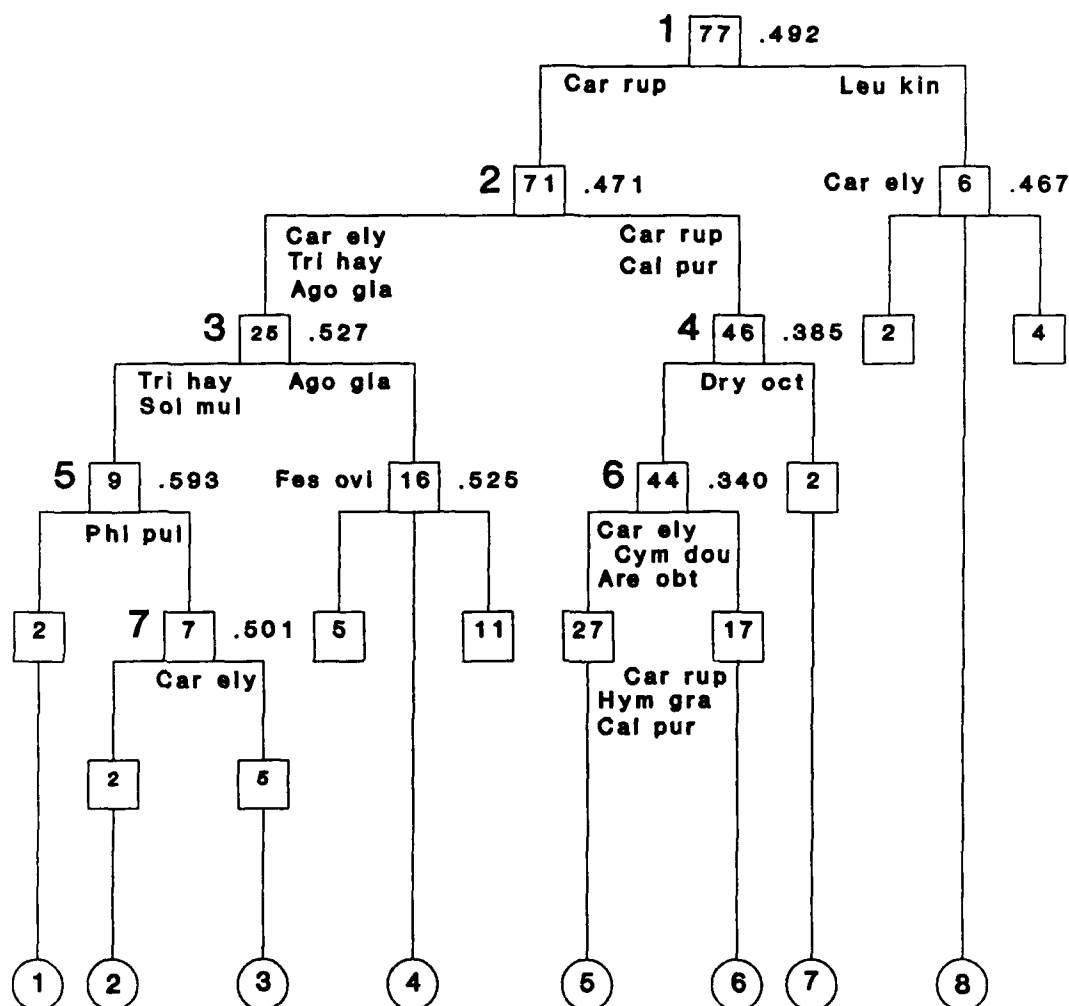


Fig. 2. TWINSpan dendrogram. Large numbers to the left of boxes are division numbers referenced in the text. Number of plots prior to division is indicated in the box, and the eigenvalue associated with the division is to the right of the box. TWINSpan indicator species, species that were highly preferential to one side of the dichotomy, are shown for each division. Circled numbers refer to group numbers as also discussed in the text. (1) *Salix nivalis*, (2) *Solidago multiradiata*-*Trifolium haydenii*, (3) *Carex elynoides*-*Trifolium haydenii*, (4) *Carex elynoides*, (5) *Calamagrostis purpurascens*-*Carex elynoides*, (6) *Carex rupestris*, (7) *Dryas octopetala*, (8) *Leucopoa kingii*.

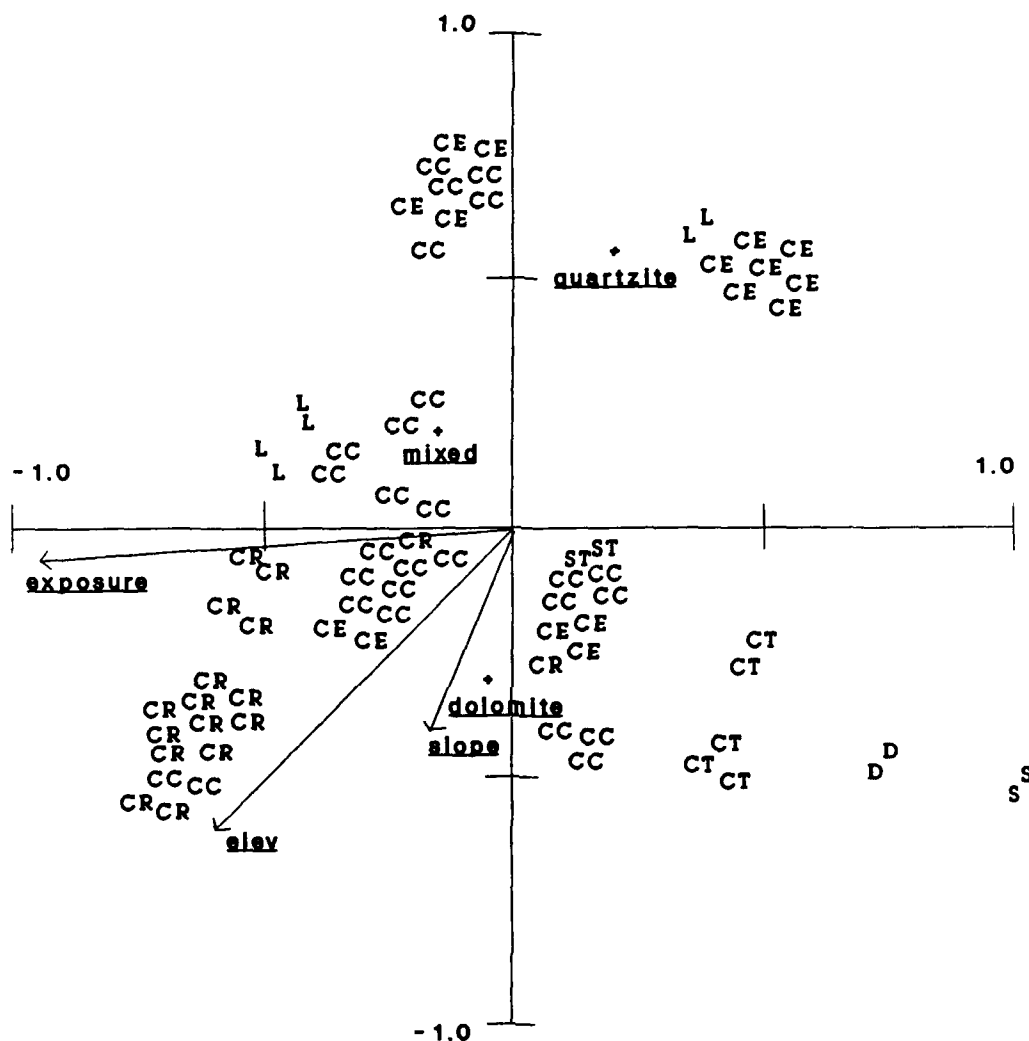


Fig. 3. CCA ordination of plots. Letters represent community membership. (S) *Salix nivalis*, (ST) *Solidago multiradiata-Trifolium haydenii*, (CT) *Carex elynoides-Trifolium haydenii*, (CE) *Carex elynoides*, (CC) *Calamagrostis purpurascens-Carex elynoides*, (CR) *Carex rupestris*, (D) *Dryas octopetala*, (L) *Leucopoa kingii*.

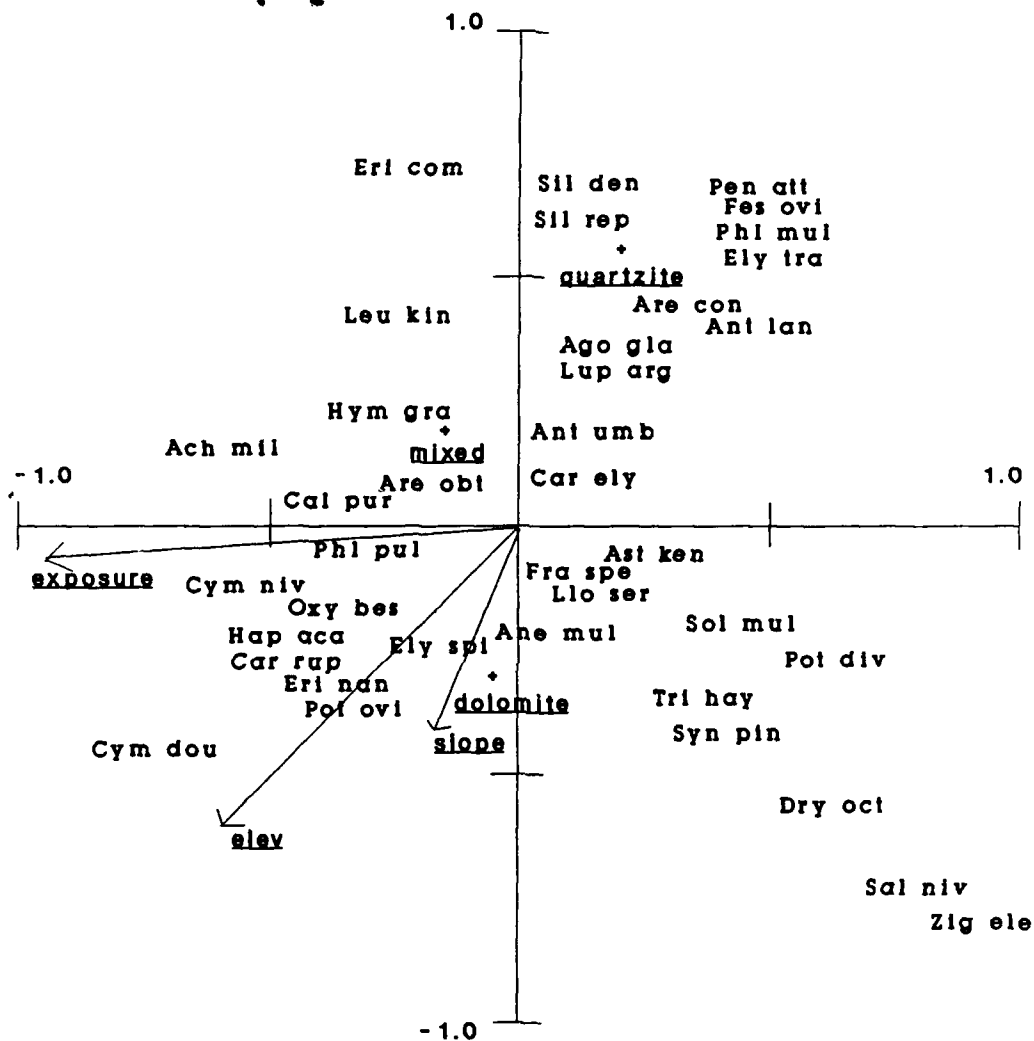


Fig. 4. CCA ordination of species. Abbreviations are explained in Table 1.

axes, display 62.5% of the total variation in all the axes of the CCA ordination (total constrained $e = 1.20$).

The plot ordination has the *Salix nivalis* community located in the least exposed, right position, while the *Carex rupestris* community occupies the exposed, left side of the diagram. In between are the remaining communities, which are further differentiated by substrate and elevation. The environmental variables failed to distinguish two communities, *Carex elynoides* and *Calamagrostis purpurascens*-*Carex elynoides*, from each other; both communities are concentrated in the middle of the plot and span both substrates. The rest of the communities are well distinguished and will be discussed in detail.

The species ordination also reflects the dominant exposure gradient. *Zigadenus elegans* and *Salix nivalis* var. *nivalis* occupy the extreme right, least exposed position and *Cymopterus douglassii*, *Achillea millefolium* var. *alpicola*, and *Cymopterus nivalis* occupy the left. The elevation arrow shows *Cymopterus douglassii*, a regional endemic, to be the highest elevation plant collected, while at the opposite extreme is a collection of many species, the most abundant being *Selaginella densa* and *Festuca ovina* var. *brevifolia*. Only *Selaginella densa*, *Erigeron compositus* var. *glabratus*, *Penstemon attenuatus* var. *pseudoprocerus*, *Festuca ovina* var. *brevifolia*, *Phlox multiflora*, and *Elymus trachycaulus* were collected solely on quartzite. The rest of the species were collected on dolomite or both quartzite and dolomite substrates.

DISCUSSION

Groupings Based on TWINSpan

Group 1: Salix nivalis ($N = 2$). This community was located on a shelf (slope = 11°) (see Appendix 4) at the base of a steep ridge, and was clearly associated with persistent snowbanks, drainage from which kept the soil waterlogged during the majority of the growing season (exposure index = 1). Vegetation cover was high (70%) with *Salix nivalis* accounting for 32%. The location was well-protected from the prevailing westerly winds due to a north-northeast aspect (elevation 3024 m). Soil development was moderate on a dolomite substrate. Other important species present were *Carex elynoides* (15%), *Solidago multiradiata* var. *scopulorum* (7%), *Zigadenus elegans* (4%), *Potentilla diversifolia* (3%), and *Astragalus kentrophyta* var. *implexus* (3%).

From the CCA analysis, the *Salix nivalis* group is the least exposed, wettest community sampled. It has two species, *Salix nivalis* and *Zigadenus elegans*, that occupy the same low exposure position in the species ordination, but the community also contains some species, especially *Carex elynoides*, with more general distributions. This community, and the *Dryas octopetala* community, were the only ones associated with persistent snowbanks at the time of sampling. The TWINSpan divisions (Fig. 2) distinguishing Group 1 from the other mesic sites had high eigenvalues, especially Division 5 ($e = 0.593$), highlighting the uniqueness of this community. Group 1 is also characterized by the near absence of the ubiquitous *Phlox pulvinata*, again revealing the extreme mesic nature of the group as compared to the rest of the study area.

Regional studies show *Salix nivalis* communities to be common in east-central Idaho (Brunsfield 1981), but replaced by *Salix arctica* in the Pioneer Mountains at the

western edge of east-central Idaho (Caicco 1983). Brunsfeld's observations support our description of this group as having a mesic habitat preference and occurring in dense mats wherever there is abundant, persistent water. *Salix nivalis* is not mentioned by Moseley (1985), but he was specifically examining *Leucopoa kingii* distributions and discusses other communities only if closely associated with *Leucopoa kingii*.

Beyond Idaho, *Salix nivalis* is widely distributed, occurring in southwestern Canada and then south through much of the western U.S. (Hitchcock and Cronquist 1973). As a dominant, it has been reported in the northern Cascades (Douglas and Bliss 1977) as occupying a generally more exposed, drier habitat, but a mesic habitat in Glacier National Park (Choate and Habeck 1967), Jasper National Park, Alberta (Hrapko and La Roi 1978), and California (Major and Taylor 1977). Noticeably absent from this list is the nearby Beartooth Plateau (Johnson and Billings 1962) and Uinta Mountains (Lewis 1970), where *Salix nivalis* apparently occurs in only small numbers.

Group 2: Solidago multiradiata-Trifolium haydenii ($N = 2$). This community was observed in a snow-collecting depression (slope = 3°) (see Appendix 4) on a northwest aspect at 2999 m. Vegetation cover was 61%, with *Solidago multiradiata* var. *scopulorum* at 21% and *Trifolium haydenii* at 17%. All of the snow had melted prior to the sampling, and no additional drainage from other snowbanks was evident; the plots were scored a 3 on the moisture index, reflecting average exposure conditions. The soil was moderately developed from a dolomite substrate. Other important species present were *Phlox pulvinata* (4%) and *Frasera speciosa* (3%).

In the TWINSpan dendrogram (Fig. 2), Group 2 initially branches with Group 3, *Carex elynoides-Trifolium haydenii*, but is separated from Group 3 at Division 7 ($e =$

0.501), mostly due to the conspicuous absence of *Carex elynoides*. These two groups were located in adjacent areas, and *Carex elynoides* was locally common in the areas around both groups. The absence of *Carex elynoides* suggests an abrupt environmental change, and it is suspected, but not observed, that this is due to a later date of snowmelt in Group 2. Group 3 is more mesic, but this results more from patterns of snowmelt drainage than to snow accumulation.

In the CCA plot diagram (Fig. 3), Group 2 occurs near the centroid for all environmental variables. *Solidago multiradiata* and *Trifolium haydenii* are in the lower right quadrant in the species ordination (Fig. 4), indicating a preference for low exposure, dolomite substrates, and average study area elevations.

Brunsfeld (1981) found *Solidago multiradiata*, which occurs throughout the western North American cordillera (Hitchcock and Cronquist 1973), on rocky, wet soils, and Caicco (1983) discusses a *Deschampsia cespitosa* (L.) Beauv. grassland in which *Solidago multiradiata* occurs with moderate abundance, but no mention is made of a community as described above. *Trifolium haydenii* is a regional endemic known only from southwestern Montana and adjacent Wyoming until recently discovered in east-central Idaho; it occupies a variety of forest and alpine habitats (Henderson 1978).

Group 3: Carex elynoides-Trifolium haydenii ($N = 5$). This community occupies a north-northwest, relatively steep slope (24°) (see Appendix 4) on dolomite, at an elevation of 3018 to 3060 m. At 80% vegetation coverage, it had the most cover of any group. *Carex elynoides* was present at 36% cover, and *Trifolium haydenii* had 23% coverage. Snow, although not present during sampling, appears to accumulate in large amounts both above and below the community, while the community itself is covered, but

not deeply so, in winter. The well-developed soil was wet during sampling; many solifluction terraces were observed. The snow drainage pattern, the high vegetation cover, and the northerly aspect resulted in a score of 2 on the exposure index, indicating a greater than average moisture condition. Other important species were *Phlox pulvinata* (7%) and *Synthyris pinnatifida* var. *canescens* (3%).

The community is positioned in the lower right quadrant of the CCA plot ordination (Fig. 3), indicating low exposure, medium altitude, and a dolomite substrate. The species ordination (Fig. 4) shows *Trifolium haydenii* as preferential to the mesic sites, while *Carex elynoides* has a more general habitat requirement, occurring in all but the driest, most exposed sites.

Other Idaho studies have encountered *Carex elynoides*, an alpine species found in the central Rocky Mountains south of Canada (Hitchcock and Cronquist 1973), to be occasional to common, but never in association with *Trifolium haydenii*, a regional endemic (Brunsfield 1981, Caicco 1983, Moseley 1985). In the southern Rocky Mountains, many communities composed of *Carex elynoides* and a species of *Trifolium* have been described, with *Trifolium dasyphyllum* T. & G. instead of *Trifolium haydenii* (Komárková and Webber 1978, Baker 1983, Eddleman and Ward 1984).

Group 4: Carex elynoides (N = 16). *Carex elynoides* turf is abundant in the study area. This community occurred on all aspects and on both dolomite and quartzite substrates. The sampling elevation was 3005 to 3054 m, and the mean slope and exposure index were 8.5° and 2.6, respectively. *Carex elynoides* by far dominated the community with 29% coverage, total vegetation coverage being 59%. *Phlox pulvinata* and *Agoseris glauca* were also important components with 5% and 2%, respectively.

Habitat preference, as revealed in the plot ordination (Fig. 3), tended toward the exposure centroid, but with wide dispersion in substrate and elevation. This community was found in areas not directly exposed to winter winds, with some snow accumulation, moderate slope (see Appendix 4), and a well-developed soil. The species ordination reveals *Carex elynoides* as a generalist, being located near the centroid.

Previous Idaho studies have identified *Carex elynoides* communities as occasional to common, with a habitat preference similar to the above description (Brunsfield 1981, Caicco 1983, Moseley 1985). *Carex elynoides* is generally restricted to alpine and occurs in the central Rocky Mountains south of Canada (Hitchcock and Cronquist 1973). It is well described as a community dominant within this area, e.g., Bamberg and Major 1968, Lewis 1970, and Baker 1983. Komárková and Webber (1978) and Willard (1979) characterize the habitat as warm, dry, southern aspects and snow-covered in the winter. Our observations agree with warm, generally dry, and a winter snow cover, but within the study area, *Carex elynoides* communities are predominately southerly in aspect, although not exclusively so.

A phase of the *Carex elynoides* turf was highlighted by the TWINSpan analysis (Fig. 2) when a small group of five plots was further delimited ($e = 0.525$) with *Festuca ovina* var. *brevifolia* as the indicator species. These plots were sampled in depressions or drainage areas and suggest a higher moisture phase of the *Carex elynoides* turf (exposure index = 2), with *Festuca ovina* var. *brevifolia* locally abundant (cover = 16%). *Festuca ovina* is a common species in the alpine of east-central Idaho, but was limited to this community in the study area. Caicco (1983) and Moseley (1985) do not mention this phase of the *Carex elynoides* community, but Lewis (1970) reports *Festuca ovina* as

important in *Carex elynoides* communities in the Uinta Mountains, and Billings and Bliss (1959) and Johnson and Billings (1962) both found *Festuca ovina* associated with snowbanks that melt prior to early July.

Group 5: Calamagrostis purpurascens-Carex elynoides ($N = 27$). This community was the largest in total number of plots and total area and was found on westerly aspects, with an average slope of 12° (see Appendix 4) and elevations 3005 to 3133 m. The habitat is generally more exposed (average exposure index = 3.4) than the *Carex elynoides* turf with *Calamagrostis purpurascens* and *Carex elynoides* each accounting for 14% of the total 57% vegetation coverage. Both dolomite and quartzite substrates are represented, but the predominate substrate is dolomite. Other important plants were *Carex rupestris* (8%), *Phlox pulvinata* (7%), *Arenaria obtusiloba* (2%), and *Hymenoxys grandiflora* (2%).

In the TWINSpan analysis (Fig. 2), this group separated early from the other two *Carex elynoides* communities (Division 2, $e = 0.471$). It is distinctive because of the large component of *Calamagrostis purpurascens*, as well as *Carex rupestris*, *Arenaria obtusiloba*, and *Hymenoxys grandiflora*, all four almost completely restricted to this community. The CCA plot ordination (Fig. 3) has Group 5 positioned near the centroid for exposure, but widely dispersed relative to the other environmental factors. The environmental variables measured do not distinguish between Groups 4 and 5, but field observations suggest that *Calamagrostis purpurascens-Carex elynoides* plots occurred in the more exposed, drier sites. In fact, on one ridge in the study area, a *Calamagrostis purpurascens-Carex elynoides* community dominated the exposed northwest aspect, while a *Carex elynoides* community was restricted to the partially protected southeast aspect. At

its upper boundaries, Group 5 grades into a *Carex rupestris* community (Group 6), which dominates dry, exposed ridgetops. *Calamagrostis purpurascens* is located near the centroid in the species ordination (Fig. 4).

Although Brunsfeld (1981) reported *Calamagrostis purpurascens* to be rare in his alpine study area, collections of the junior author and others at the University of Idaho Herbarium document it as common, especially on calcareous substrates. Moseley (1985) reported one alpine community in which *Calamagrostis purpurascens* was dominant, but it was not an important component of the alpine communities studied by Caicco (1983). Hitchcock and Cronquist (1973) describe its distribution as low elevation to subalpine in much of northern and northwestern North America. Douglas and Bliss (1977) found *Calamagrostis purpurascens* communities to be frequent in the northern Cascades, and Willard (1979) mentions *Calamagrostis purpurascens* as strongly associated with *Carex elynoides* turf.

Group 6: Carex rupestris ($N = 17$). The *Carex rupestris* community occupied the highest, driest, most exposed sites in the study area. The elevation ranged from 3011 to 3146 m, and the exposure index was 3.9. All sites are likely snow-free in winter, and all have shallow, rocky soil derived from dolomite. The average slope was 16° (see Appendix 4), but a great deal of variation exists between sites, some occurring on flat ridge tops, while others were on steep inclines. Overall, these communities are sparsely vegetated (35%); most of the area was exposed mineral soil. *Carex rupestris* accounted for 16% of the vegetation coverage, *Phlox pulvinata* 4%, with *Calamagrostis purpurascens* and *Cymopterus douglassii* minor components.

The plot ordination (Fig. 3) further emphasizes the relatively extreme habitat favored by this group, with the *Carex rupestris* plots occurring in the bottom left quadrant indicating high exposure, high elevation, and a dolomite-derived soil. The species ordination (Fig. 4) shows *Carex rupestris* in a less extreme position, due to its presence in other communities, but *Cymopterus douglassii* maintains an outlier position. *Cymopterus douglassii* is a highly restricted endemic presently known only from the alpine of the Sheep Mountain RNA and a few alpine/subalpine sites in the vicinity of Mt. Borah, some 47 km southwest in the Lost River Range, Custer County, Idaho. It is only present in the community in the highest elevation sites, while *Calamagrostis purpurascens* becomes more important at lower elevations close to the ecotone between Groups 5 and 6.

Caicco (1983) found only one small example of this community in the Pioneer Mountains, and Moseley (1985) did not encounter it at all in east-central Idaho. This group appears to be rare in Idaho, but it was well-represented in our sampling. *Carex rupestris* is widely distributed throughout Alaska and Canada and south along the Rocky Mountains to Utah and Colorado (Hitchcock and Cronquist 1973), and has been reported as a dominant in the Big Snowy Range of Montana (Bamberg and Major 1968), the Uinta Mountains of Utah (Lewis 1970), Rocky Mountain National Park, Colorado (Willard 1979), and on Wheeler Peak, New Mexico (Baker 1983). All these studies report *Carex rupestris* communities occurring in xeric, exposed sites, as observed in this study.

Group 7: Dryas octopetala ($N = 2$). This community was represented by only two plots in one small location on rocky, dolomitic soil at an elevation of 3048 m. The site is characterized by a steep slope (26°) (see Appendix 4), and a protected, low exposure, northeasterly aspect. The community occurred just below a ridgetop with

persistent snowbanks 10 m upslope observed draining through the community (exposure index = 1.5). The vegetation cover was 65% with *Dryas octopetala* var. *hookeriana* accounting for 45%; other important species were *Lupinus argenteus* var. *depressus* (9%) and *Carex rupestris* (7%).

In the plot ordination (Fig. 3), Group 7 is located in the lower, right quadrant, indicating a relatively low exposure, dolomite habitat preference. The same preference is evident in the species ordination (Fig. 4), with *Dryas octopetala* exceeded as an outlier by only two other species, *Salix nivalis* var. *nivalis* and *Zigadenus elegans*.

Brunsfeld (1981) collected *Dryas octopetala* in east-central Idaho, and described it as occasional, with a preference for rocky, calcareous substrates and protected, snow-covered ridges, but it was not reported by either Caicco (1983) or Moseley (1985).

Dryas octopetala is widespread in Arctic and Boreal regions, south into the Rocky Mountains, and is reported to form communities occupying a wide variety of habitats within this range. It is often found on rocky, calcareous slopes, but some report xeric, exposed, snow-free habitats (Bamberg and Major 1968, Knapik et al. 1973, Komárková and Webber 1978, and Spence and Shaw 1981), while others report protected, less dry, sites with some snow cover in winter (Hrapko and La Roi 1973, Douglas and Bliss 1977). Eddleman and Ward (1984) observed a *Dryas octopetala* community in the Colorado Front Range with conditions nearly identical to those in our study, i.e., a rocky, wet soil fed by snow meltwater.

Group 8: Leucopoa kingii ($N = 6$). By species composition, this group was recognized as unique by TWINSpan (Fig. 2) in the first division ($e = 0.492$), with the *Leucopoa kingii* communities being separated from the rest. A subsequent division

further divided it into two recognizable phases, a stable and an unstable phase, essentially as characterized by Moseley (1985).

The stable phase was found on a mesic, well-developed soil derived from quartzite with moderate slope (12°) (see Appendix 4), an elevation of 3011 m, and a southwest aspect (exposure index = 2). Vegetation coverage was 70%, with *Leucopoa kingii* at 12%; other important species were *Carex elynoides* (34%) and *Lupinus argenteus* var. *depressus* (6%).

The unstable phase was present on a much drier, loose, rocky, dolomite substrate with a steep slope (27°) (see Appendix 4), an elevation of 3036 m, and a west aspect (exposure index = 4). Vegetation coverage was 42%, with *Leucopoa kingii* at 22%; other important species were *Achillea millefolium* var. *alpicola* (4%) and *Cymopterus nivalis* (3%).

The plot ordination (Fig. 3) highlights the differences in the two phases in this group. The stable phase is in the upper-right quadrant, revealing a low exposure, quartzite preference, while the unstable phase occupies the lower portion of the upper-left quadrant, indicating a high exposure, dolomitic habitat.

Both phases are well-described in Moseley's (1985) investigation of the *Leucopoa kingii* communities of east-central Idaho. Caicco (1983) also observed a few, small *Leucopoa kingii* communities in the White Knob Mountains.

Leucopoa kingii occurs throughout the northwest U.S., from low elevations to the alpine, but has not been found to be a prominent member of alpine communities except for the Wasatch Mountains in Utah (Ream 1964, cited in Moseley 1985), central and east-central Idaho (Caicco 1983, Moseley 1985), and the present study.

Environmental factors. The measured environmental variables were helpful in describing the community distributions, but did not distinguish between two communities, *Carex elynoides* and *Calamagrostis purpurascens-Carex elynoides*. An exposure gradient, determined by factors such as slope, aspect, snow accumulation/drainage patterns, and soil characteristics, was highly correlated with the first axis and accounted for the majority of the variation observed. Even though the study area has a limited elevation range, elevation was still correlated with both axes 1 and 2 and was helpful in interpreting community and species distributions. Substrate was strongly correlated with the second axis, and accounted for a substantial amount of the variation. Some communities were restricted to one substrate, while others were found on both dolomitic and quartzitic substrates. Caution must be used, however, in interpreting the community substrate preferences; the quartzite bands in the study area are in relatively protected, lower elevation depressions and so represent an environmental contrast to the immediately adjacent dolomite plots, independent of the substrate. Slope was also important, especially in the *Leucopoa kingii* community, and was correlated with the third axis (see Appendix 4).

Caicco (1983) also describes a "complex moisture-exposure gradient" in his ordinations of central Idaho alpine, as well as a "geographical" axis related to clusters of plots in his large study area. In east-central Idaho, Moseley (1985) again recognized a moisture-exposure gradient as important. In addition, he identified species composition changes with changes in substrate (limestone vs nonlimestone) and soil stability.

That exposure was found to be important in the distribution of Idaho alpine is no surprise. Billings (1973) clearly describes a "mesotopographic gradient" that explains all

the exposure factors found in our study, e.g., slope, aspect, snow accumulation, drainage. More recently, Isard (1986) thoroughly investigated topographical environmental influences on Niwot Ridge, Colorado, and again, vegetation distribution was found to be dependent on snow accumulation and drainage patterns.

East-central Idaho supports a well-developed, recognizable alpine vegetation. The present study focused on one such alpine site and found eight distinctive communities, which were described on the basis of habitat preference. An exposure gradient was found to be most highly correlated with the observed variation in habitat preferences, but elevation, substrate, and slope were also important. In general, the study area communities present a uniformly dry turf-like physiognomy, with some early snowbed and *Dryas* or *Salix* mat communities occasionally present. This is in sharp contrast to the other regional alpine studies, where fellfields and meadows are also common. Winds, topography, and precipitation patterns appear to be creating a relatively dry alpine habitat; substantial drought stress was obvious at the completion of sampling on 25 July. Drought conditions may help explain the absence of wet meadows, but not the lack of fellfields dominated by cushion plants. These unique features warrant further investigation.

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APPENDIX 1
SAMPLING METHODS
AND DATA ANALYSIS

Sampling methods. The selection of a homogeneous stand involves finding an area of uniform vegetation that is also uniform with respect to substrate type and animal disturbance (Daubenmire 1959). The stand is then sampled by the stratified-random layout of quadrats as previously described. The Daubenmire quadrat (1959) is a rectangle, 20 x 50 cm, marked with references for 5, 25, 50, 75, and 100 percent cover. A polygon is visualized that contains all of the branches of the individual plant or clump of plants under consideration, and its percent cover is estimated. Then, the percent cover of all of the polygons of the same species are added together to obtain the percent cover for the species. Due to overlap in the canopies of the different species, the total percent cover for a quadrat is not expected to equal 100%. The size of the quadrat optimizes the visual estimate because it is the proper size to be viewed without having to move one's eyes. A smaller size would require many more samples to get a fair representation of the plot.

Visual estimates of cover are appropriate in the alpine, and have been used successfully by many researchers (Ratcliffe and Turkington 1987, Welden 1985, Baker 1983, Bliss 1963, and Douglas and Bliss 1977). Accuracy can be a problem when visual estimates are used due to the differences in conspicuousness of each species and the observer's familiarity with the vegetation, or even the observer's mental state (Grieg-Smith 1983). Only a reasonable level of accuracy is required, however, because all values are averaged over the 20 quadrats of the plot and then reduced to either the TWINSpan cutlevels or the Octave Scale for CCA. For example, all values over 20% are treated equally in the TWINSpan analysis. Additionally, the species list and associated abundances for any one plot represent a substantial amount of information. If

one species is under or over estimated, the computer analysis will still recognize the plot as being either unique or similar to other plots. Sampled within-stand variation must be smaller than between-stand variation (Gauch 1982). Given the extremes of environmental gradients in the alpine, coupled with preferential selection of sampled stands, this is assured.

A search of the literature reveals that preferential selection of stands is the most common sample placement method used by alpine plant ecologists. All of the studies referred to in this paper utilized preferential selection, and I am not aware of any that do not use a preferential sampling scheme. Other alternatives, e.g., random, regular, stratified (Gauch 1982), are possible, but are not useful or practical for alpine community studies. Abrupt changes along environmental gradients in alpine areas are often accompanied by equally abrupt changes in community composition. Some communities are very large, while others with unique habitat preferences can be very small, e.g., snowbed or talus. Only preferential selection of representative homogeneous stands can guarantee that all communities will be sampled and described, unless a massive sampling project is undertaken.

The combination of the Daubenmire quadrat method with preferential selection of stands creates an efficient and sufficiently accurate technique for describing alpine vegetation. I began sampling in the alpine as early as the vegetation permitted, continued sampling for five weeks, at the end of which the vegetation was browning from drought stress. In other words, alpine researchers must deal with a time factor that has to be considered in the method. The technique utilized must have only the accuracy required to

accomplish the objective, so as to be able to get the most samples possible within the limitations of the growing season.

For the computer analysis, only species with greater than 2% average coverage in at least one of the 77 plots were included. This decision was made for time efficiency reasons, since it cut down on the specimen collecting and identifying load, and species with such low abundances represent an insignificant proportion of the information in a plot.

Detrended correspondence analysis (DCA). I had initially intended to use DCA in combination with CCA to analyze the data, as recommended by Ter Braak (1987). DCA (Hill and Gauch 1980) is an ordination method utilizing reciprocal averaging to arrange the plots on the basis of species present and species abundances. Similar plots are in close proximity when plotted against the ordination axes. Uncorrected reciprocal averaging has the problem that information on the second axis is distorted into an arch. In addition, the distortion causes compression of the ordination space at the two ends of the first axis. To correct these problems, DCA was developed and all tests with artificial and field data initially seemed to support its effectiveness (Hill and Gauch 1980). The arch distortion is corrected by compressing the second axis by averaging second axis scores within small segments of the first axis and then subtracting the mean from each score. The compression problem is also fixed by manipulating the ordination; areas toward the ends of the first axis are expanded and the center is contracted (Gauch 1982).

In my study, DCA would have been useful as a comparison to the CCA ordination. A DCA ordination is derived from the species data alone, without being constrained by environmental factors, as is the case in CCA. If the eigenvalue of each axis of the CCA

is not substantially less than the DCA eigenvalues, then the researcher assumes no important environmental variable has been missed (Ter Braak 1986).

The problem with comparing CCA and DCA ordinations is that DCA has come under increased scrutiny and criticism. Since originally being introduced, its sensitivity to rare species has always been recognized (Hill and Gauch 1980), but more serious problems have since been discovered. In an extensive test with simulated data, Minchin (1987) found DCA to be too sensitive to deviations in a unimodal response curve and often to cause "distortions," even with the required model. He suggests a possible cause could be the detrending or suppression of the second axis arch and the rescaling or expansion of the ends of the first axis. Wartenberg et al. (1987) continued the criticism by arguing that the arch is in fact not a distortion, but an important aspect of the data and should not be corrected. They also criticized the rescaling as arbitrary and artifactual. Peet et al. (1988) came to the defense of DCA, but, I feel, to no avail, because they argued for its continued use based on the lack of alternatives, not on its theoretical advantages.

Recently, Jackson and Somers (1991) have presented a convincing argument against the use of DCA. They tested DCA using artificial data with different variations of the segmentation used in the arch correction. The results were dependent on the number of segments used; an option of DECORANA (Hill 1979a) allows the user to select the number of segments to be used in the analysis. Obviously, if different results can be obtained by simply changing the number of segments, the method is neither robust nor helpful in explaining ecologic data.

My experience with DCA, as performed by CANOCO (Ter Braak 1987-1992), supports the recommendation against using DCA. In Jongman et al. (1987), Ter Braak

suggests deleting rare species from the DCA ordination so that the DCA results will be comparable to the CCA ordination. Remember that DCA is susceptible to distortion by rare species, but CCA generally is not (Ter Braak 1987). I produced four ordinations with DCA, each time deleting rare species. First, I deleted all species with only one occurrence in the 77 plots sampled. Then I deleted species with only two occurrences and so on. I also deleted some plots in which the deleted rare species represented a substantial portion of the vegetation. For each of the plots, rank correlation coefficients were calculated (an option of CANOCO) between the plot scores and measured environmental variables. The interpretation of the first axis was stable, but the interpretation of the problematic second axis was definitely unstable. With each level of deletion, the second axis interpretation changed from initially being an exposure/substrate gradient, to slope, to exposure, and then finally back again to exposure/substrate. Additionally, the eigenvalues of all axes decreased with each deletion, e.g., the first axis decreased from 0.624 to 0.555. This is to be expected since deleting rare species effectively reduces the variation in the data, but it skews the comparison to the CCA ordination. If the goal is to compare the two ordinations to determine if the important environmental variables have been accounted for, then it seems unreasonably arbitrary to delete a subjectively selected number of rare species, reduce the DCA eigenvalues, and then make the comparison.

Based on all of the above arguments, I decided that the DCA analysis should not be included in my overall interpretation of the data.

TWINSPAN analysis (Hill 1979b). All default values were used with the TWINSPAN analysis except the maximum number of divisions was limited to five, an option that does

not influence the interpretation. The default TWINSpan cutlevels de-emphasize abundant species, allowing less abundant species to have some influence on the classification. Since TWINSpan is based on reciprocal averaging, theoretically it is sensitive to rare species; consequently, the option to delete rare species and how many to delete could influence the outcome.

To address this possibility, I followed the same approach used in the DCA analysis. I consecutively deleted rare species starting with species with only one occurrence up to species with three occurrences. The resulting TWINSpan groupings were stable in their interpretation. They were identical, in fact, except when species with only three occurrences were deleted; five plots out of 77 were grouped differently from the other scenarios. All five plots were located in the immediate vicinity of ecotones, and the change was due to the loss of information. The overall interpretation was still the same; TWINSpan appears to be stable in this respect. I used the original analysis with all species included to describe the plot groupings.

Canonical correspondence analysis (CCA). For the CCA analysis, the species data were transformed to the Octave Scale (0-9) (Gauch 1977). A logarithmic transformation is recommended when the data are skewed by inclusion of some very large numbers (Ter Braak 1987). The transformation prevents the analysis from being dominated by the most abundant species. Specifically, the Octave Scale is logarithmic to the base 2, e.g., percent cover in the range 16 to 32 is converted to a 7. The environmental data were also considered for transformation, but none was accomplished, since all of the individual environmental factors had an acceptable distribution in their original form.

Because CCA is based on reciprocal averaging, it can also be susceptible to the arch problem and the associated compression of the first axis ends (Ter Braak 1987). As many axes can be derived by CCA as there are environmental variables in the analysis. If the number of environmental variables approaches the number of plots, then CCA becomes reciprocal averaging. Detrending, as in DCA, is available in the program CANOCO, but Ter Braak (1990) does not recommend its use because of possible "numerical problems." A better way to avoid the arch problem is to limit the analysis to only the "essential" environmental variables (Ter Braak and Prentice 1988). Nonessential variables can be recognized by deleting variables that are most significant with respect to the second axis (Ter Braak 1987). For my analysis, substrate was highly correlated with the second axis. I deleted dolomite, quartzite, and mixed from the ordination with the result that the interpretation was the same, minus the substrate. The deletion had little effect on the groupings of plots or the interpretation of axes.

Additionally, if only the essential variables are included, this time determined by correlation with at least one of the ordination axes, then the arch distortion is "not likely to occur at all" (Ter Braak and Prentice 1988, p. 294). Only the mixed class of substrate in my analysis fits this description. I did an ordination with the mixed class deleted, as well as the two plots in that class, with the result of no change in the ordination diagram, except those two plots were missing.

An obvious check for arch distortion is to see if an arch is visually present in the ordination diagram; figure 3 does not reveal an arch pattern. For my analysis, only six environmental factors were included, and arch distortion does not appear to be a problem.

Another reciprocal averaging drawback, outlier sensitivity, is potentially a problem in CCA, but only if the plot with rare species is also extreme in its environmental variables (Ter Braak and Prentice 1988). A plot with these conditions would cause distortion in the ordination by compressing other plots into a smaller area of the diagram (Gauch 1982). Again, looking at Figure 3, this does not appear to be a problem. The same protocol used with TWINSpan and DCA was also followed for CCA; a series of ordinations was accomplished with rare species being deleted. The ordination diagram was exceptionally robust to the manipulations and the interpretations were the same with only one exception; the third axis with species with only three occurrences deleted did not have a clear interpretation, where in the other scenarios, it was highly correlated with slope. Intuitively, the slope interpretation fits the actual species distribution the best, e.g., stable versus unstable *Leucopoa kingii* communities (see Appendix 4).

Overall, CCA proved to be exceptionally robust when compared to DCA. All of the above manipulations, almost without exception, led to the same interpretation of the data. I used the original ordinations, with all information included, to analyze the community and species variation.

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APPENDIX 2
FIELD OBSERVATION RECORDS

SPECIES DATA IN CORNELL CONDENSED FORMAT

38 77SHEEP MT

TCSHMT**

(18,9(13,F5.0))

9

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2 10 16.0 1 5.0 2 4.0 9 3.0
3 3 6.0 10 5.0 8 21.0 2 4.0 1 3.0
4 3 8.0 10 4.0 8 18.0 2 4.0 1 4.0
5 13 35.0 14 3.0 3 16.0 11 4.0 7 2.0 15 5.0
6 13 28.0 14 3.0 3 14.0 11 3.0 7 3.0 15 9.0
7 1 5.0 2 3.0 10 18.0
8 1 3.0 2 4.0 10 13.0 8 2.0
9 1 4.0 2 4.0 10 16.0
10 19 11.0 3 32.0 22 3.0 18 3.0 20 3.0
11 19 6.0 3 25.0 18 4.0 20 17.0 17 4.0 1 3.0
12 19 5.0 3 42.0 18 4.0 20 7.0 17 5.0 1 5.0
13 10 16.0 1 5.0 4 3.0 28 2.0 38 2.0
14 10 10.0 1 3.0 4 3.0 8 3.0
15 3 7.0 21 15.0 23 6.0 16 4.0 25 5.0 22 5.0 24 2.0
16 3 27.0 21 16.0 25 3.0 24 6.0
17 3 34.0 21 14.0 23 10.0 22 3.0
18 1 7.0 9 5.0 10 9.0 38 3.0 8 3.0 5 4.0
19 1 7.0 9 3.0 10 8.0 8 3.0 5 5.0
20 3 13.0 1 12.0 9 2.0 10 2.0 38 2.0 8 3.0 5 10.0
21 3 5.0 1 11.0 9 3.0 10 4.0 8 3.0 5 6.0
22 21 20.0 3 32.0 1 3.0 22 3.0
23 3 43.0 1 14.0 20 2.0 18 6.0
24 3 13.0 10 19.0 8 10.0 20 2.0 18 9.0 1 8.0 19 3.0 38 4.0
25 3 41.0 18 3.0 1 11.0 19 5.0 17 4.0
26 3 32.0 8 21.0 6 2.0 18 3.0 1 3.0 7 5.0
27 3 31.0 8 28.0 6 3.0 18 2.0 7 4.0 38 2.0
28 3 17.0 8 31.0 6 3.0 18 5.0 1 2.0 38 3.0 9 2.0
29 3 11.0 10 19.0 8 8.0 1 7.0 38 3.0 18 6.0 9 3.0
30 3 8.0 10 13.0 8 20.0 1 3.0 38 4.0 18 5.0 9 2.0
31 3 3.0 10 5.0 8 27.0 1 5.0 38 2.0 18 8.0 7 2.0 5 2.0
32 8 11.0 10 10.0 3 14.0 1 13.0 38 2.0 6 3.0
33 8 26.0 10 3.0 3 15.0 38 4.0 6 6.0 9 3.0 7 2.0 5 3.0
34 8 15.0 10 20.0 3 5.0 1 4.0 5 5.0 6 5.0 7 5.0 38 3.0
35 8 31.0 10 16.0 3 5.0 1 4.0 5 3.0 6 4.0 7 3.0 38 4.0
36 8 16.0 3 6.0 10 17.0 6 3.0 1 7.0 7 2.0
37 8 20.0 10 13.0 6 2.0 1 15.0 5 4.0
38 8 8.0 3 30.0 1 14.0 38 3.0 6 2.0
39 8 6.0 3 24.0 1 11.0 38 3.0 28 4.0
40 8 21.0 3 33.0 10 4.0 1 6.0 16 5.0 38 3.0 9 3.0

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 42 3 34.0 1 11.0 15 3.0 21 5.0 30 6.0
 43 3 17.0 21 14.0 14 7.0 29 2.0
 44 20 12.0 19 8.0 31 5.0 1 2.0
 45 20 7.0 31 6.0
 46 20 35.0 19 3.0 31 6.0 28 8.0 17 4.0
 47 20 33.0 28 3.0 1 4.0
 48 32 42.0 10 9.0 19 6.0 7 3.0
 49 32 47.0 10 4.0 19 12.0 7 2.0 13 3.0
 50 10 23.0 3 7.0 1 2.0 8 2.0
 51 10 18.0 3 8.0 1 3.0 8 4.0
 52 10 14.0
 53 10 20.0 2 3.0
 54 10 15.0 1 5.0 2 4.0
 55 10 15.0 1 5.0 2 3.0
 56 10 23.0 8 7.0 1 6.0 5 2.0 28 6.0
 57 10 17.0 8 4.0 1 5.0 4 2.0
 58 3 29.0 8 13.0 33 4.0 1 7.0 6 2.0 22 4.0 4 3.0
 59 3 27.0 33 17.0 1 3.0 22 2.0 4 3.0
 60 3 39.0 33 4.0 1 7.0 22 3.0 4 7.0
 61 3 27.0 34 3.0 22 2.0 28 6.0
 62 3 20.0 28 3.0 20 4.0 4 2.0 35 2.0 33 5.0
 63 8 10.0 3 31.0 20 4.0 19 2.0 1 4.0 36 2.0 22 3.0 6 2.0
 64 3 29.0 20 10.0 19 3.0 1 10.0 22 2.0 10 12.0
 65 10 14.0 3 9.0 1 8.0 5 2.0 6 2.0
 66 10 15.0 3 14.0 1 6.0 5 3.0 6 2.0 8 3.0
 67 3 66.0 26 16.0 38 2.0 1 8.0 34 3.0
 68 3 13.0 26 17.0 1 9.0 34 4.0 10 23.0
 69 3 26.0 26 41.0 1 6.0 34 4.0 14 7.0
 70 3 43.0 26 25.0 15 15.0 1 4.0 34 2.0
 71 3 32.0 26 17.0 1 8.0 34 3.0 14 3.0 38 2.0 23 2.0
 72 10 23.0 8 9.0 26 2.0 1 3.0 33 11.0
 73 10 10.0 8 17.0 1 2.0 3 7.0
 74 10 8.0 3 15.0 8 5.0 1 12.0 4 3.0 38 3.0 6 2.0
 75 3 28.0 8 7.0 1 6.0 38 2.0 6 3.0 37 2.0
 76 15 23.0 26 19.0 25 2.0 12 3.0 27 2.0 1 2.0
 77 15 19.0 26 15.0 27 4.0 1 6.0 19 3.0

0
 PHL PUL CYM DOU CAR ELY POT OVI ERI NAN HYM GRA AST KEN CAL PUR OXY BES CAR RUP
 ZIG ELE LLO SER SAL NIV POT DIV SOL MUL ANT UMB SIL REP SEL DEN LUP ARG LEU KIN
 FES OVI AGO GLA ANT LAN PHL MUL ARE CON TRI HAY FRA SPE CYM NIV PEN ATT ELY TRA
 ACH MIL DRY OCT ELY SPI SYN PIN HAP ACA ERI COM ANE MUL ARE OBT
 1 2 3 4 5 6 7 8 9 10
 11 12 13 14 15 16 17 18 19 20
 21 22 23 24 25 26 27 28 29 30
 31 32 33 34 35 36 37 38 39 40
 41 42 43 44 45 46 47 48 49 50
 51 52 53 54 55 56 57 58 59 60
 61 62 63 64 65 66 67 68 69 70
 71 72 73 74 75 76 77

ENVIRONMENTAL DATA IN CORNELL CONDENSED FORMAT

6 77SHPENVIR
(15,1X,11,F3.0,1X,11,F5.0,1X,11,F4.0,1X,11,F2.0)

TCSHEN**

4

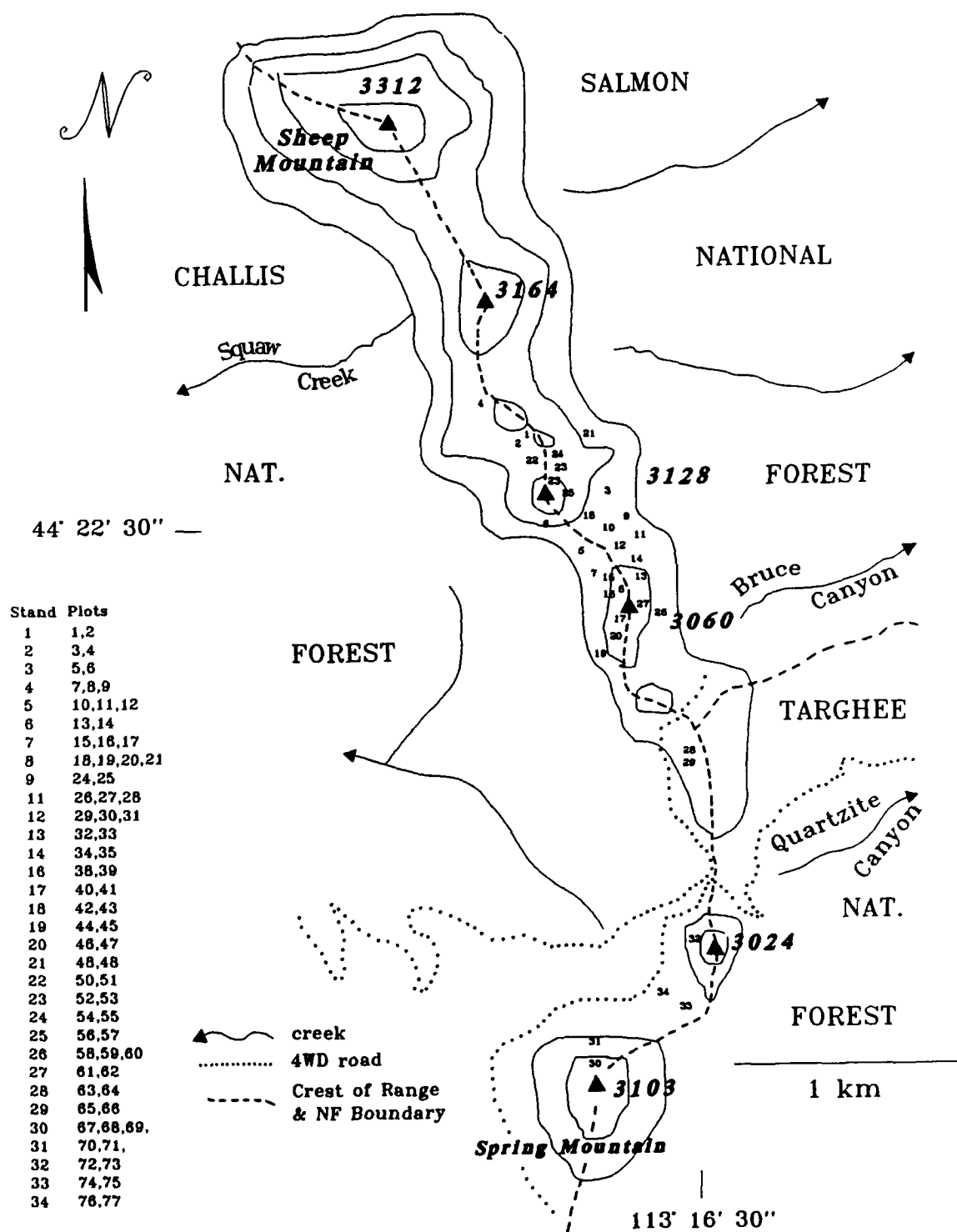
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3 1 13 2 3133 3 4.0 4 1
4 1 13 2 3133 3 4.0 4 1
5 1 11 2 3024 3 1.0 4 1
6 1 11 2 3024 3 1.0 4 1
7 1 18 2 3133 3 4.0 4 1
8 1 18 2 3133 3 4.0 4 1
9 1 18 2 3133 3 4.0 4 1
10 1 12 2 3011 3 2.0 5 1
11 1 12 2 3011 3 2.0 5 1
12 1 12 2 3011 3 2.0 5 1
13 1 27 2 3072 3 4.0 4 1
14 1 27 2 3072 3 4.0 4 1
15 1 3 2 3005 3 2.0 5 1
16 1 3 2 3005 3 2.0 5 1
17 1 3 2 3005 3 2.0 5 1
18 1 9 2 3054 3 3.0 4 1
19 1 9 2 3054 3 3.0 4 1
20 1 9 2 3054 3 3.0 4 1
21 1 9 2 3054 3 3.0 4 1
22 1 8 2 3005 3 2.0 5 1
23 1 4 2 3008 3 3.0 5 1
24 1 9 2 3008 3 3.0 5 1
25 1 9 2 3008 3 3.0 5 1
26 1 7 2 3005 3 3.0 5 1
27 1 7 2 3005 3 3.0 5 1
28 1 7 2 3005 3 3.0 5 1
29 1 7 2 3021 3 3.0 5 1
30 1 7 2 3021 3 3.0 6 1
31 1 7 2 3021 3 3.0 6 1
32 1 14 2 3036 3 3.5 4 1
33 1 14 2 3036 3 3.5 4 1
34 1 11 2 3024 3 3.0 4 1
35 1 11 2 3024 3 3.0 4 1
36 1 16 2 3018 3 3.5 4 1
37 1 16 2 3018 3 3.5 4 1
38 1 26 2 3024 3 3.5 4 1
39 1 26 2 3024 3 3.5 4 1
40 1 18 2 3042 3 3.5 4 1

41 1 18 2 3042 3 3.5 4 1
 42 1 6 2 3011 3 2.0 5 1
 43 1 6 2 3011 3 2.0 5 1
 44 1 26 2 3024 3 4.0 4 1
 45 1 26 2 3024 3 4.0 4 1
 46 1 27 2 3048 3 4.0 4 1
 47 1 27 2 3048 3 4.0 4 1
 48 1 26 2 3048 3 1.5 4 1
 49 1 26 2 3048 3 1.5 4 1
 50 1 6 2 3109 3 4.0 4 1
 51 1 6 2 3109 3 4.0 4 1
 52 1 16 2 3121 3 4.0 4 1
 53 1 16 2 3121 3 4.0 4 1
 54 1 19 2 3133 3 4.0 4 1
 55 1 19 2 3133 3 4.0 4 1
 56 1 28 2 3109 3 4.0 4 1
 57 1 28 2 3109 3 4.0 4 1
 58 1 8 2 3036 3 3.0 4 1
 59 1 8 2 3036 3 3.0 4 1
 60 1 8 2 3036 3 3.0 4 1
 61 1 18 2 3054 3 3.5 4 1
 62 1 18 2 3054 3 3.5 4 1
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 64 1 10 2 3005 3 3.0 5 1
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 68 1 23 2 3060 3 2.0 4 1
 69 1 23 2 3060 3 2.0 4 1
 70 1 25 2 3018 3 2.0 4 1
 71 1 25 2 3018 3 2.0 4 1
 72 1 13 2 3011 3 3.5 4 1
 73 1 13 2 3011 3 3.5 4 1
 74 1 4 2 3008 3 3.0 4 1
 75 1 4 2 3008 3 3.0 4 1
 76 1 3 2 2999 3 3.0 4 1
 77 1 3 2 2999 3 3.0 4 1

0

SLOPE	ELEV	EXPOSURE	DOLOMITE	QUARTZ	MIXED				
1	2	3	4	5	6	7	8	9	10
11	12	13	14	15	16	17	18	19	20
21	22	23	24	25	26	27	28	29	30
31	32	33	34	35	36	37	38	39	40
41	42	43	44	45	46	47	48	49	50
51	52	53	54	55	56	57	58	59	60
61	62	63	64	65	66	67	68	69	70
71	72	73	74	75	76	77			

PLOT LOCATIONS



APPENDIX 3
TWINSpan OUTPUT

77666774111212246556666222233334 1223333334667771155557 1555544114444
56677890135672035248901234678901350348012467891563453401672127899234589124567

14	POT	DIV	22	---	3-23	-----	00000
11	ZIG	ELE	22	-----		00001	
12	LLO	SER	--2	-----		00001	
13	SAL	NIV	55	-----	-2	00001	
15	SOL	MUL	3354	---4	---2	00001	
26	TRI	HAY	--4444554	-----	-2	00001	
27	FRA	SPE	--22	-----		00001	
34	SYN	PIN	---22222	-----	-2	00001	
21	FES	OVI	-----44445	---3	-----	00010	
22	AGO	GLA	-----3-222	---22222-2	-----	00010	
23	ANT	LAN	-----2-3-4	-----		00010	
24	PHL	MUL	-----23	-----		00010	
25	ARE	CON	--2	-----32	-----	00010	
29	PEN	ATT	-----2	-----		00010	
30	ELY	TRA	-----3	-----		00010	
35	HAP	ACA	-----2	-----		00010	
36	ERI	COM	-----2	-----		00010	
4	POT	OVI	-----223-2	-----2-22	---2	00011	
16	ANT	UMB	-----2	-----3	-----	00011	
33	ELY	SPI	-----242-3	-----4	-----	00011	
6	HYM	GRA	-----2	---2-222	---32-----23222--22-22	0010	
7	AST	KEN	22	-----32	---222-----32-----22	0010	
37	ANE	MUL	-----2	-----		0010	
38	ARE	OBT	---2	---2-----2-22222222--22-22--222--222	-----	0010	
5	ERI	NAN	-----222	---243-3-2--22	-----2-2--3	00110	
8	CAL	PUR	-----4	---4455535555555542224445332-2433-2223233	---2-2	00110	
9	OXY	BES	-----222-2-2-322	-----32	---2	00110	
2	CYM	DOU	-----22	-----22222--222	-----	00111	
10	CAR	RUP	---5	---4	---4---443242323224544--44443-4454545444443454432	00111	
32	DRY	OCT	-----55	-----		00111	
1	PHL	PUL	--2333323	---2-4444323--232-2323-2322344423444332433222332233223--33--232--2		01	
3	CAR	ELY	44	---54555435555555555555455443243533-43433-55534345--33	---55	01	
18	SEL	DEN	-----232	-----3223333	-----22	01	
17	SIL	REP	-----2	-----		10	
19	LUP	ARG	---2	---4-3-2--22	-----34333-2	10	
20	LEU	KIN	-----22	---4---222	-----434355	10	
31	ACH	MIL	-----333	-----		10	
28	CYM	NIV	-----32	-----2	---2---3	32	

[illegible]

APPENDIX 4
CCA ORDINATION OF PLOTS FOR
SECOND AND THIRD AXES

Letters represent community membership: (S) *Salix nivalis*; (ST) *Solidago multiradiata*-*Trifolium haydenii*; (CT) *Carex elynoides*-*Trifolium haydenii*; (CE) *Carex elynoides*; (CC) *Calamagrostis purpurascens*-*Carex elynoides*; (CR) *Carex rupestris*; (D) *Dryas octopetala*; (L) *Leucopoa kingii*.

